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Wet heathlands of the southern Swan Coastal Plain, Western Australia: A phytosociological study

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Abstract

Wet heathlands, formed by sclerophyllous nanophanerophytes and graminoids growing on seasonally waterlogged soil, were surveyed on the southern Swan Coastal Plain and classified using two-way indicator species analysis (TWINSPAN). Three main wet heathland groups were identified, these being the *Pericalymma - Hypocalymma*, *Pericalymma - Regelia* and *Melaleuca - Cassytha* alliances respectively. The *Pericalymma - Hypocalymma* alliance is found north of the Capel River in depressions in the Bassendean Dune system on colluvial sands which have impermeable organic, clay or ferruginous horizons at about a metre. The *Pericalymma - Regelia* alliance is found south of the Capel River primarily on colluvial wet sands, and shallow sands and loams, in the Abba soil association. Variations in vegetation composition within this alliance are associated with the depth to the impermeable layer (usually lateritic) and the winter height of the perched water table. The *Melaleuca - Cassytha* alliance was found north of the Capel River mainly on heavy clays formed from Quarternary alluvium within the Serpentine River Association. These heathlands were species poor compared to Australian dry heathlands, with the number of species per 100 m^2 ranging from 9 to 26. The ecology of these heathlands is discussed in the light of the limited information available. Their existence as fragmented islands within a primarily agricultural landscape makes them vulnerable to changes in ecosystem processes.

Introduction

Wet heathlands, which are plant formations dominated by evergreen sclerophyllous nanophanerophytes and graminoids growing on seasonally waterlogged soil (Groves & Specht 1965; Specht 1981), are widespread but of very limited area in the south west of Western Australia. Dry heathland, now generally termed kwongan, has been the subject of much scientific research in Western Australia over the last ten years (*e.g.* Brown & Hopkins 1983; Pate & Beard 1984; Bell & Loneragan 1985; Brown 1989), but wet heathland remains largely undescribed in regard to its phytosociology and ecology. Undoubtedly this is because wet heathland in Western Australia is much less extensive and less species rich than dry heathland.

Dry heathland or kwongan, most of which occurs on sandplain soils in the low to moderate (300-600 mm) rainfall areas of the South West Botanical Province, has been estimated to cover 118,000 km^2, or 27% of the province (Beard 1984). No comparable estimate of the area of wet heathland, which is virtually confined to the high rainfall (> 800 mm) areas of the south-west, is available. Because of its limited and scattered occurrence, wet heathland has usually been mapped in conjunction with sedgeland and "swamp vegetation" (Smith 1973; Beard 1981).

The dry heathland of the sandplains is extremely species rich at small (< 1 ha) sample sizes with an average of 60 species per 100 m^2 in the central wheatbelt (Brown 1989) and 70 per 100 m^2 in the lateritic uplands of the Mt Lesueur area (Hopkins & Griffin 1984). There are few published reports of species richness in Western Australian wet heathland. Wardell-Johnson *et al.* (1989) found an average of 21 species per 314 m^2 plot in a heathland community on damp shallow sandy sites near Walpole on the south-western coast. However, this study did not include herbaceous perennials and some annuals.

Much of the vegetation which originally included wet heathland communities has been cleared for agriculture and the area of this vegetation type left in Western Australia would probably cover no more than 500 km^2, with the most extensive areas being within the Warren Botanical Subdistrict (Smith 1972). The wet heathland of the southern Swan Coastal Plain (SCP), which is the focus of this study, is primarily restricted to small conservation reserves and road verges surrounded by cleared farmland.

The main objective of this study was to characterize the wet heathland communities of the southern SCP in terms of their characteristic species and to relate these communities to soil and other environmental factors. Identification of the community types provides a framework to plan the management and conservation of these communities, which despite their relative paucity of species provide a habitat for many of the rare and endangered plant taxa of the high rainfall areas of the South West Botanical Province (Keighery & Robinson 1990).

Regional Setting

Geology, Geomorphology and Soils

All study sites were on the southern part of the Swan Coastal Plain (SCP), Western Australia, between latitude 33° 00' S and 33° 45' S (Fig 1). The SCP extends from the Darling and Whicher Scarps to the Indian Ocean and to about 60 m above sea level. The plain is underlain by the Phanerozoic sediments of the Perth Basin and several landform units lying parallel to the coastline and closely related to the geology can be identified (Wilde & Walker 1982). At the foot of the Darling Scarp is a zone comprised of coalesced colluvial fans and the remnants of a strandline deposit. This zone merges into a 10 km-wide alluvial plain (often called the Pinjarra Plain), which has been lateritized and then extensively stripped to form soils which are predominately meadow podzolic in nature (Mulcahy 1973). The meadow podzols consist of a sandy surface overlying a poorly structured clay of low permeability developed on a lateritic pallid zone. Along the streams which cross the plain, younger deposits in the form of terraces are incised into the meadow podzols and in places alluvial fans overly them. These younger soils are red and yellow podzolics and undifferentiated soils.

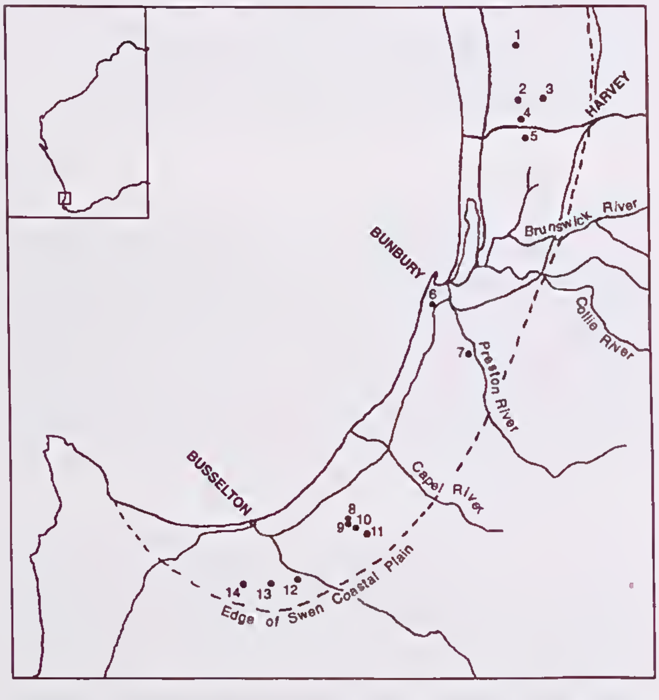

Figure 1. Wet heathland vegetation survey areas on the southern Swan Coastal Plain. 1. Riverdale Nature Reserve, 2. Reserve No. 20331, 3. Wellard Nature Reserve, 4. Guthrie Forest Block, 5. Byrd Swamp Nature Reserve, 6. Hay Park Recreation Reserve, 7. Reserve No. 1167, 8. Ruabon Nature Reserve, 9. Ruabon (railway reserve), 10. Williams Road (railway reserve), 11. Tutunup (railway reserve), 12. Yoongarillup Reserve, 13. Fish Road Reserve, 14. Ambergate Nature Reserve.

Further west, at least three generations of dune soils, overlying the fluviatile deposits, are evident. At the present coastline is the youngest dune system, the Quindalup System of McArthur & Bettenay (1960), which consists of highly calcareous shell sand deposited during the Holocene. Inland of this system lies a belt of slightly podzolized yellow sand overlying limestone called the Spearwood System (McArthur & Bettenay 1960). The Spearwood sands are almost entirely quartz although there are localized deposits of heavy mineral sands. Lying between the Spearwood System and the alluvial plain is the Bassendean System (McArthur & Bettenay 1960), composed of the oldest aeolian deposits, which have now lost their dune morphology. It is of lower relief than the younger dunes nearer the coast and the soils are highly leached and podzolized white quartz sands with B horizons of accumulated iron and organic matter. The depressions between these low dunes are filled with swamp and lacustrine deposits which may be peat, peaty sand, sand or clay (Wilde & Walker 1982).

Details of the soil associations of the three dune systems and the alluvial plain for the southern SCP are given by McArthur & Bettenay (1956, 1958), Pym & Poutsma (1957), McArthur (1958) and Tille & Lantzke (1990).

Climate

The climate of the area is "mediterranean" with cool wet winters and warm to hot, dry, summers (Gentilli 1972). Proximity to the coast provides a moderating influence and frosts are infrequent, with mean temperatures of the coldest and hottest months being 11-13°C and 25-29°C. Mean annual rainfall ranges from about 850 to 1000 mm through the study area with the higher levels occurring near the scarps. The pasture growing season is seven months, from April to October inclusive, and during this period the excess of rainfall over potential evapotranspiration of pastures is 560 mm at Harvey (Pym & Poutsma 1957) and 380 mm at Bunbury (McArthur & Bettenay 1956). This excess of water is available for run-off, storage in the sub-soil or penetration to the underlying aquifers. The flat topography of much of the coastal plain ensures that there is little run-off and where the subsoils are relatively impermeable much of this excess is probably stored in the subsoil and therefore is available for growth of deep rooted native species beyond the period of pasture growth (McArthur & Bettenay 1956).

Methods

Data collection

The fourteen reserve and roadside sites containing areas of wet heathland were visited, usually at least twice, in spring 1992 and 1993. At each site between three and eight 10 m x 10 m quadrats were sampled. Within each quadrat, all vascular plant species were either identified in the field or given a code number and collected for later identification. The nomenclature of Green (1985) and Marchant *et al.* (1987) was used. Each species was given a cover value between 1 and 5 on a modified Braun-Blanquet scale: 1, <5%; 2, 5-25%; 3, 25-50%; 4, 50-75%; 5, 75-100%. At least one soil pit was dug at each site down to 1 metre, or to a limiting horizon. Soil texture of each horizon was recorded and samples were taken within each horizon for determination of the Munsell colour. Published soil surveys were also used to determine the soil type at each site and note was taken at the time of survey of the depth of watertable at each site.

Data analysis

Vegetation data were classified by two-way indicator species analysis using the polythetic divisive computer program TWINSPAN (Hill 1979) and the Braun-Blanquet cover value for each species. Only the 116 species which were found in at least two quadrats were used in the analysis. In general, classification was terminated at the third level of division to give three groups (alliances) and six subgroups (associations) of the 47 quadrats; a further sub-group was recognized at the fourth level of division. Groupings of less than four quadrats at the fourth level of division were not recognized. The taxonomic composition of the species groups was compared using the Sorenson coefficient of community (Gauch & Whittaker 1972). Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) was used to ordinate the 47 quadrats so their relationship with identified edaphic variables could be examined.

Results

Vegetation and soils

The TWINSPAN classification produced three main groups of wet heathland species, which are termed **alliances** in this paper and seven sub-groups or **associations** (Appendix 1). Two of the groups, the *Pericalymma-Hypocalymma* alliance, with two associations, and the *Pericalymma-Regelia* alliance, with three associations, contain the shrub *Pericalymma ellipticum* as one of the characteristic species. The other main wet heathland group, the *Melaleuca-Cassytha* alliance which is divided into two associations, does not contain *P. ellipticum* but is usually dominated by shrubs of *Melaleuca* spp., the most characteristic of which is *M. incana*. The climber *Cassytha glabella* is also a characteristic component of these heathlands. In general the *Pericalymma-Hypocalymma* alliance is found on deep sands (humus podzols), with organic depositional layers at 1 to 1.5 metres, north of the Capel River and the *Pericalymma-Regelia* alliance is found on a range of soils from deep sand to shallow loams, usually with a laterite hardpan at less than a metre, south of the Capel River. The *Melaleuca-Cassytha* alliance is found on deep clays or sand over clay north of the Capel River. The typical soils for each of the associations are summarized in Table 1.

Similarity of alliances, associations and quadrats

The Sorensen coefficients of community of the various alliances and associations are given in Table 2. This coefficient, which has a maximum value of 200 when the two samples being compared have all their species in common,

Table 1
Soil descriptions for wet heathland communities of the southern Swan Coastal Plain.

Association	Soil Description
***Pericalymma-Hypocalymma* alliance**	
P. ellipticum-H. angustifolium-Hibbertia vaginata [A1]	Deep (> 1 m) light grey[1] sand sometimes with an organic deposition hardpan at 1 to 1.5 m. High organic matter content in A1 horizon [Uc 2.33][2]. Top soil[1]-C/N ratio: moderate-high (23-27), P (total): very low (20-30 ppm), pH: strongly acid (5.0-5.5)[3].
P. ellipticum-Evandra pauciflora-Hypolaena exsulca [A2]	Deep (> 1 m) light grey to greyish brown sand sometimes with an organic deposition or laterite hardpan at 1 to 1.5 m [Uc 2.31]. High organic matter content in A1 horizon. Top soil-C/N ratio: moderate-high (23-27), P (total): very low (20-30 ppm), pH: strongly acid (4.9-5.5).
***Pericalymma-Regelia* alliance**	
P. ellipticum-R. ciliata-Leptocarpus canus [B1]	Pale brown, brown or grey sand to sandy loam over laterite hardpan at 0.25-1 m [Uc 2.21]. Top soil-C/N ratio: low-moderate (18-21), P (total): very low-low (40-70 ppm), pH: moderately acid (5.4-6.1).
P. ellipticum-Chamelaucium roycei-Grevillea diversifolia [B2]	Dark reddish brown loam to greyish brown or brown sandy loam over laterite hardpan at 0.1 to 0.5 m [Um 5.21/Uc 5.11]. Top soil-C/N ratio: low (16-18), P (total) very low to high (40-400 ppm), pH: moderately acid (5.4-5.9).
P. ellipticum-Kunzea recurva-Daviesia preissii [B3]	Deep (>1 m) light grey fine sand to grey brown sandy loam over laterite caprock at 1 to 1.5 m [Uc 2.21]. High organic matter content in A1 horizon. Top soil-C/N ratio moderate to high (23-28), P (total) very low (40-50 ppm), pH moderately acid (5.5-5.9).
***Melaleuca-Cassytha* alliance**	
M. viminea-Isolepsis nodosa-C. glabella [C1]	Deep (>1m) greyish brown to light yellowish brown heavy clay [Ug 5.14]. Top soil: C/N ratio very low-low (9-17), P (total) low-moderate (40-120 ppm), pH strongly-moderately acid (4.8-6.2).
M. incana-M. hamulosa-K. recurva [C2]	Deep (> 1 m) grey brown sand overlying very pale brown sandy clay [Uc 1.21]. Top soil: moderately acid (5.5-6.0), may have high salt content.

[1] Soil colour according to Munsell colour charts. [2] Northcote (1975) soil classification. [3] Soil chemical data from Pym & Poutsma (1957), McArthur & Bettenay (1956, 1958), McArthur (1991) and Smith 1994.

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summarizes the similarity in composition of the species groups. Although structurally the three wet heathland alliances have the same variants (heathland-sedgeland, heathland and tall heathland), the similarity between alliances based on shared species is relatively low with Sorensen's coefficients of community between 16 and 22. This indicates a high degree of beta diversity despite quite low species richness. Even within alliances, the highest coefficient is 49 and it is generally lower than 32.

of the *Pericalymma-Hypocalymma* alliance. The third axis (not shown) divided the *P. ellipticum-R. ciliata-L. canus* and *P. ellipticum-K. recurva-D. preissii* association quadrats at one end (high values) from the *P. ellipticum-C. roycei-G. diversifolia* association (low values) with the *Pericalymma-Regelia* alliance quadrats occupying intermediate values. Unfortunately, because soil data were not recorded from each quadrat, it is not possible to more precisely relate values on the DCA axes to edaphic variables.

Table 2

Total species numbers and Sorenson coefficients of community of the wet heathland alliances and associations.

Alliance	A	B	C
A *Pericalymma-Hypocalymma* (56 spp.)	–	21.6	16.8
B *Pericalymma-Regelia* (120 spp.)		–	17.6
C *Melaleuca-Cassytha* (39 spp.)			–

Association	A1	A2	B1	B2	B3	C1	C2
A1 (33 spp.)	–	49.2	21.7	12.3	18.9	13.6	3.9
A2 (28 spp.)		–	21.0	7.9	23.2	14.8	4.3
B1 (96 spp.)			–	29.2	30.6	12.9	7.0
B2 (48 spp.)				–	18.0	8.1	6.1
B3 (41 spp.)					–	14.9	10.2
C1 (26 spp.)						–	31.8
C2 (18 spp.)							–

The eigenvalues of the first four axes of the DCA were 0.74, 0.39, 0.29 and 0.22. The DCA clearly divided the 47 quadrats into the three major alliances and reinforced the outcome of the classification (Fig 2). It also confirmed the greater similarity of the *Pericalymma-Hypocalymma* and *Pericalymma-Regelia* alliances to each other than each has with the *Melaleuca-Cassytha* alliance. The values along the major axes appear to be related to the soil types at the wet heathland sites. The highest values on axis 1 correspond with the deep clays of the Wellard and Byrd Swamp nature reserves, with slightly lower values associated with the deep sands over clay at Hay Park. Low values on both axis 1 and axis 2 are associated with the shallow sandy loams and loams of the Tutunup-Ruabon area. An increase in value on axis 2 appears to correspond with an increase in soil depth and increasing sandiness of the soil, with the highest values occurring at reserve ↑1167 which has deep grey sands, but which also has a higher cover of sedges than the other sites

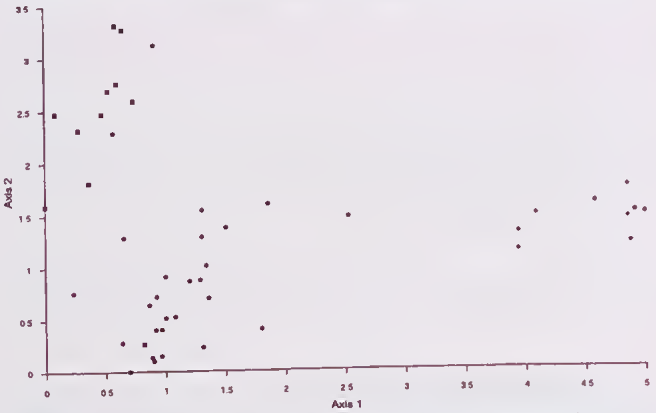

Figure 2. Detrended Correspondence Analysis ordination (axes 1 & 2) of 47 wet heathland quadrats from the southern Swan Coastal Plain showing the three alliances derived from the TWINSPAN classification. ■ *Pericalymma-Hypocalymma* alliance, • *Pericalymma-Regelia* alliance, ◆ *Melaleuca-Cassytha* alliance.

Description of associations

The *Pericalymma-Hypocalymma* alliance. The *P. ellipticum-Hypocalymma angustifolium-Hibbertia vaginata* association (association A1 in Appendix 1, Table 1) is found on the deep acid grey sands (Joel series and related Swamp types) of the Bassendean Association (Pym & Poutsma 1957) in the northern part of the study area. These soils have an organic B horizon, which may be concreted to form a hardpan, at 1 to 1.5 metres. It is probably the most extensive of the wet heathland formations on the southern SCP being found in State Forest on the east side of the McLarty and Myalup Plantations and in nature reserves in the Kemerton area. The wetlands in which this heathland association are found occur as regularly spaced depressions, or interdune swales, and are classed as sumplands (seasonally inundated basins) of the Riverdale suite by Semeniuk (1988). Recharge of the sumplands is by precipitation or groundwater rise. Structurally, the association is mid-dense to closed heathland (Walker 1983) dominated by shrubs up to about 1 m with varying amounts of graminoids up to about 25% of ground cover and in some places emergent *Xanthorrhoea preissii*, *Melaleuca preissiana* or *Nuytsia floribunda*. The heathlands grade into *Eucalyptus marginata-E. calophylla* open forest on low sandy rises, *M. rhaphiophylla* and *M. preissiana* low forest in wetter areas, and *E. gomphocephala-E. marginata* forest on the sands of the Karrakatta Association to the west.

The *P. ellipticum-Evandra pauciflora-H. exsulca* association (A2) is found on similar soils and topographical positions to the association described above, and they have many species in common. The main difference is the greater dominance of *P. ellipticum* and the larger proportion of the Cyperaceae and Restionaceae in the *P. ellipticum-E. pauciflora-H. exsulca* association which may indicate that the sites are somewhat wetter. This association is found in State Forest west of

Harvey, and on several small reserves in the same area and also south of Bunbury. In the Harvey area, the soils are of the Joel series and related types of the Bassendean Association, and in the Bunbury-Capel area they are the Swamp series VI of the Southern River Association (McArthur and Bettenay 1956). The presence of organic or ferruginous hardpans at about 1 metre as found in some of these soils may account for the increased proportion of graminoids characteristic of this association. Structurally, the association is a mid-dense to closed heathland, generally below 1.2 metres tall, with occasional emergent *Kunzea ericifolia* or *M. preissiana*. It may grade into a low forest of *M. preissiana* or a sedgeland dominated by *E. pauciflora* in wetter areas and into *E. marginata-E. calophylla* forest or *K. ericifolia* tall shrubland or *Banksia attenuata* woodland on interswale dunes.

The *Pericalymma-Regelia* alliance. The *P. ellipticum-Regelia ciliata-Leptocarpus canus* association (B1) is the most widespread group within this alliance, being found on the Wet Sand soil type of the Abba Wet Ironstone Flats land unit (Tille & Lantzke 1990). These acid grey sands are similar to the Joel Sand of the Bassendean Association and have a similar origin. They may grade into the Bog Iron Ore Sand of Tille and Lantzke (1990) when the laterite hardpan comes to within less than 50 cm of the surface. The heathlands of this association occupy a similar position topographically to the Joel Sand of the Bassendean Association being found in shallow depressions and swales in areas of sandplain and low dune fields. The association is restricted to road verges and three small (<200 ha) nature reserves between Tutunup and Ambergate south of Busselton. The structure of the mature formation is mid-dense to closed heathland which varies in average height from 0.6 to 1.2 m but may be up to 1.6-1.8 m (tall heathland) in some areas. The species richness of the shorter heathland, particularly that at the Ruabon Nature Reserve and part of the Fish Road Nature Reserve, is only about half of that of the taller heathland. In other areas, with deeper soils, species characteristic of the association such as *Melaleuca uncinata, M. hamulosa, Hakea varia, R. ciliata* may grow to more than 2 metres high. At Tutunup the association merges quite sharply with *E. calophylla* forest, which has an almost completely different suite of species in the understorey, and is situated on the low rises interspersed with the heathlands. The soils on these rises are deep (1.5-2.0 m) Abba and Busselton sands (Tille & Lantzke 1990).

The *P. ellipticum-Chamelaucium roycei-Grevillea diversifolia* association (B2) is perhaps the most restricted unit in the *Pericalymma-Regelia* alliance. It is confined to shallow loams over laterite hardpan along a road and rail reserve in the Tutunup area southeast of Busselton and covers less than 10 hectares. The soils are the Bog Iron Ore Loams of the Abba Wet Ironstone Flats land unit (Tille & Lantzke 1990) with less than 30 cm of brown loam overlying a massive laterite hardpan. This association merges with the *P. ellipticum-R. ciliata-L. canus* association which occurs where the laterite is deeper than about 30 cm and the loam gives way to loamy sand and sand. It is wetter than the latter association and sometimes water stands several centimetres deep above the soil surface over the winter months. The drainage along the verge has been modified by road and railway construction, the latter taking place over 120 years ago. The declared endangered species *C. roycei* is characteristic of this association. Several undescribed taxa including species of *Loxocarya, Restio* and *Dryandra* are also found. Structurally the association is closed heathland to tall closed heathland (Walker 1983) with emergent *Viminaria denudata, Xanthorrhoea preissii*, and various *Melaleuca* species up to 3 m high.

The *P. ellipticum-Kunzea recurva-Daviesia preissii* association (B3) differs from the other two associations within the alliance mainly in regard to the taxa that it does not have. *Regelia ciliata* is replaced by a similar myrtaceaous shrub *Kunzea recurva* and it does not have the rich cover of species in the genera *Lepyrodia, Leptocarpus, Restio* and *Loxocarya* found in the other associations. It also has a restricted distribution, being found at Ambergate and Yoongarillup on small nature reserves. At Ambergate the soils are of the Wet Sand or Busselton type (Tille & Lantzke 1990) with laterite hardpan at about 1 m, at Yoongarillup the soils are brown sandy loams over sandy clay loams (Mixed Alluvial Soils; Tille & Lantzke 1990). The *P. ellipticum-K. recurva-D. preissii* association is also a mid-dense to closed heathland with occasional emergent *X. preissii*, grading into *E. marginata-E. calophylla* forest on the slight rises surrounding the shallow depressions in which the heathland is found.

The *Melaleuca-Cassytha* alliance. The *Melaleuca viminea-Isolepsis nodosa-Cassytha glabella* association (C1) is found in the northern part of the study area on small remnants of uncleared heavy kaolinitic clays of the Serpentine River soil association (Pym & Poutsma 1957). The very low permeability of these clays and the level topography restricts drainage and water lies on the surface for several months over winter. They occur near the boundary between the Bassendean Dunes and the alluvial Pinjarra Plain and the soils were formed by the build-up of alluvium from streams terminating in the Bassendean Dunes (Semeniuk 1988). It forms a closed heathland at the Wellard Reserve and a tall heathland (1.5-2.5 m) at Byrd Swamp Reserve, with up to half of the ground cover being provided by sedges and restiads (*Isolepsis, Lepyrodia, Leptocarpus, Gahnia*) in some areas. Climbers, primarily *C. glabella*, are also prominent. On the low sandhills surrounding the heathland association occurs *Agonis flexuosa* or *Kunzea ericifolia* low forest or *E. marginata-E. calophylla* forest with an understorey of Banksia species. In wetter areas *M. rhaphiophylla* low forest with an understorey including *M. lateritia, Astartea fascicularis* and *Lepidosperma longitudinale* may be found.

Further south, near Bunbury, the *Melaleuca incana-M. hamulosa-Kunzea recurva* association occurs on deep grey sand over sandy clay. This soil is similar to the Stirling VII Sand and Swamp Series IV of McArthur & Bettenay (1956). Although it is also alluvial in origin, it is much more permeable than the clays of the *M. viminea-I. nodosa-C. glabella* association, however during winter the watertable may rise above the ground surface. This association is represented by only one site, within the city of Bunbury, although it probably occurs in other areas south of Bunbury near the junction of the Bassendean and Spearwood dune systems. It is similar structurally to the tall heathland variant of the *M. viminea-I. nodosa-C. glabella* association found at Byrd Swamp but with the sedge *Gahnia trifida* and the native grass *Sporobolus virginicus* forming the graminoid component rather than *Isolepsis* and *Lepyrodia* species. On better drained soil to the east of the heathland occurs a low woodland of *Melaleuca preissiana*.

Discussion

Comparisons with other heathlands: Species richness

The *Pericalymma-Regelia* and *Pericalymma-Hypocalymma* wet heathland alliances of the southern Swan Coastal Plain have a comparable species richness to similar communities in New South Wales and Queensland. At the 100 m^2 scale, wet heathland in Royal National Park and Ku-ring-gai Chase near Sydney averaged 23.9 and 18.0 species respectively (Specht & Specht 1989) compared to 15.8 (up to 21/100 m^2) for the *Pericalymma-Hypocalymma* alliance and 18.4 (up to 26/100 m^2) for the *Pericalymma-Regelia* alliance. However the southern SCP alliances are considerably less species rich than other coastal heathlands on sand in Western Australia. At Nornalup National Park, wet heathlands growing on similar soils had 34 species per 50 m^2 (George *et al.* 1979) and at Scott River a low open heathland on deep grey sand had 40 species per 100 m^2 (Specht & Specht 1989). The low species richness of the *Melaleuca-Cassytha* alliance and of some of the wetter areas of the other two southern SCP communities (9-12 species/100 m^2) is similar to that of the species poor heathlands of northern Europe (Gimingham *et al.* 1979).

Comparisons with other heathlands: Floristics

There are few published reports of the floristics of other wet heathlands in Western Australia, and none of these has attempted a classification of this community type. Wardell-Johnson *et al.* (1989) describe two wet heathland communities growing on humus podzols over deep sands at Nornalup near the south coast of Western Australia, called the *Beaufortia sparsa* plain and *Dasypogon bromeliifolius* heathland communities. These communities share *Adenanthos obovatus, Lysinema ciliatum, Melaleuca thymoides,* and *D. bromeliifolius* with the *Pericalymma-Hypocalymma* alliance. Havel (1968) describes a low *M. preissiana* woodland growing within the Bassendean Dune system near Perth. Apart from *M. preissiana*, this community has *P. ellipticum, A. obovatus, D. bromeliifolius* and *H. angustifolium* in common with the *Pericalymma-Hypocalymma* alliance. Keighery & Trudgeon (1992) describe several wet heathland communities growing on the SCP near Perth, which are dominated by *P. ellipticum* and which, in common with the *Pericalymma-Regelia* alliance, include *P. ellipticum, Hakea sulcata, Xanthorrhoea preissii, Stirlingia latifolia, Calothamnus lateralis* and the sedges *Mesomelaena tetragona* and *Hypolaena exsulca*. Keighery & Robinson (1990) mention wet heathlands growing on red clays and loams over laterite hardpan on the Scott Plains east of Augusta, which share a number of rare taxa with the *Pericalymma-Regelia* alliance. The *Melaleuca-Cassytha* wet heathland alliance has taxonomic affinities with low woodlands and low closed forests dominated by *M. rhaphiophylla* and *M. cuticularis* around swamps and on seasonally wet areas of the Yoongarillup Plain landform south of Perth (Trudgeon 1991; R Smith *pers. obs.*).

The remnant wet heathlands growing on the northern part of the SCP and on the Scott Plains are apparently species rich, and the bulk of the taxa occurring in them are different from those in the communities which were the subject of this study. There is a clear need for a formal classification of these communities because they are threatened by urban development and mining (Keighery & Robinson 1990; Gibson & Keighery 1992).

A comparison of the most important plant families within each of the southern SCP wet heathland alliances (Table 3) shows a very high proportion of Myrtaceae in the *Melaleuca-Cassytha* alliance. The percentage of Restionaceae in the *Pericalymma-Hypocalymma* and *Pericalymma-Regelia* alliances is about double that of the 25 mostly dry heathland sites surveyed in the south west of Western Australia by George *et al.* (1979). Except for the *Pericalymma-Regelia* alliance, the proportion of Proteaceae in the SCP heathlands is lower than most Western Australian dry heathlands (George *et al.* 1979; Brown & Hopkins 1983) where it is generally above 15%. As with most Australian heathlands, there was a low proportion of species of the Epacridaceae in the flora of the southern SCP heathlands and where they did occur they had low foliage cover values. This is in contrast to the wet heathlands of Europe and South Africa where the closely related family Ericaceae is often a dominant component of the community (Gimingham *et al.* 1979; Cowling & Holmes 1992).

Table 3

Numbers and percentage (in brackets) of species in each of the major plant families in the southern Swan Coastal Plain wet heathlands. Only those species which were positively identified have been included.

Family	*Pericalymma-Hypocalymma*	*Pericalymma-Regelia*	*Melaleuca-Cassytha*
Myrtaceae	8 (15%)	11 (12%)	11 (31%)
Proteaceae	3 (6%)	15 (21%)	3 (8%)
Leguminosae	7 (14%)	8 (8%)	5 (14%)
Restionaceae	6 (12%)	11 (12%)	3 (8%)
Cyperaceae	3 (6%)	3 (3%)	4 (11%)
Liliaceae	4 (8%)	5 (5%)	1 (3%)
Epacridaceae	3 (6%)	1 (1%)	-
Stylideaceae	1 (2%)	5 (5%)	-
Dilleneaceae	2 (4%)	4 (4%)	-
Droseraceae	2 (4%)	3 (3%)	1 (3%)
Orchidaceae	2 (4%)	-	3 (8%)

Ecological processes

Only some general comments can be made on ecological processes within the wet heathlands of the SCP as there has been little ecological research in these communities. Clearly the soil moisture regime is critical in determining the extent of the wet heathland formation and in modifying plant species composition within the formation. The *Pericalymma-Hypocalymma* and *Pericalymma-Regelia* alliances are similar to the groundwater heaths described for eastern Australia by Groves & Specht (1965) and Siddiqi *et al.* (1972) which are subjected to extremes in soil moisture availability. In the rainy season the watertable is close to the surface for several months, while during the dry season the soil above the impermeable layer of clay, peat, or laterite hardpan underlain by clay, drys out. As plant roots are generally not able to penetrate this layer, water deficits become severe in summer. The rapid drying out of these soils was illustrated by a study of watertable levels along a transect from heathland on shallow loam over laterite hardpan to woodland on deep sands at Tutunup (Smith 1994). In late August and early September, the watertable was 3 cm to 5 cm above the surface in the heathland and 5 cm to 14 cm below the surface in the woodland. By late October the watertable in the heathland had withdrawn to within or below the laterite (50 cm below the surface) and in the woodland the watertable was greater than 85 cm below the surface.

As well as the stress caused by the drying out of the relatively shallow soils in summer, high watertables in winter cause additional stress to the heathland species. Waterlogging by perched watertables causes soil air, which is essential to root respiration, to be expelled from the soil (Specht 1981). The duration of waterlogging is important in determing the species composition of wet heathlands (Webster 1962; Siddiqi *et al.* 1972). The seedlings of many sclerophyllous trees are very sensitive to prolonged waterlogging (> 2-3 months) and thus fail to establish in adjacent heathland soils whereas the seedlings of heathland plants generally have morphological or physiological adaptations which alleviate the anaerobic conditions (Specht 1981).

Few nitrifying or nitrogen-fixing bacteria can exist under the poorly aerated conditions of waterlogged soils (Woolhouse 1981) and therefore these soils may be low in available N. Inhibition of the nitrification process (Groves 1981) is indicated by the high C/N ratios (23-27) of the podzols of the *Pericalymma-Hypocalymma* alliance (Table 2). Leaching of the soils in wet heathlands may also lead to a reduction in some cations, notably Ca^{2+}, Mg^{2+} and K^{+}. Research into the ecology of European wet heathlands has shown that nutrient-poor, waterlogged sites act as refugia for slow growing plants which are not able to compete well on better aerated, fertile soils (Berendse & Aerts 1984).

A comparison of soil nutrients in the Bog Iron Ore and Wet Sand soils under wet heathland at Tutunup with those in the Abba Sand under *Eucalyptus marginata-E. calophylla* forest adjacent to them shows the heathland soils to have similar levels of total N and total P, higher extractable K and Na but substantially lower extractable Ca and Al (Smith 1994). Some of the Bog Iron Ore loams have quite high levels of total P (up to 400 ppm) but this nutrient is probably strongly bound by iron oxides and extractable P is low (McArthur 1991). The low total P concentrations of most of the wet heathland soils of the southern SCP (Table 2) are typical of Australian heathlands (Groves 1981; Keith & Myerscough 1993).

Disturbance in the wet heathlands

Most of the wet heathlands surveyed in this study occur on reserves of less than 200 ha or on narrow road reserves, and are surrounded by cleared agricultural land or pine plantations. Fragmentation of these areas of natural vegetation may have major effects on various ecological processes, such as the water and nutrient cycles, and especially in the smaller fragments, the radiation balance and wind regimes (Hobbs 1993). Clearing of the surrounding native vegetation may lead to a rise in the watertable and consequent salt accumulation near the surface, as has occurred on the lower SCP since at least the 1950's (McArthur & Bettenay 1956). Fertilizer drift from adjacent farmland may disrupt the natural nutrient cycle and encourage the invasion of exotic plants (Smith 1990).

Too frequent fire is another stress which may lead to the deterioration of natural vegetation in ecosystem fragments. Although most of the sites surveyed for this study had apparently not been burnt for 8-10 years, much of the heathland along the Tutunup-Ruabon railway was recently burnt, and was burnt for fuel reduction every few years in the past (F Negus *personal communication*). The vegetation of the wet heathlands recovers quite rapidly after fire due to the high proportion of resprouters (R Smith *personal observation*). However the post fire environment with its abundant light and increased nutrient levels in the ash bed provides an ideal seed bed for invasive weed species which may out-compete slower growing native species (Baird 1977). The combination of recurrent fire and rising salinity levels may place extra stress on the recovery of species which normally require establishment of seedlings after fire (Baird 1984).

This survey provides a systematic analysis of a community which is likely to be one of the rarer components of the Western Australian vegetation. If biodiversity is to be an important criterion for conservation of this vegetation type in this State, then the high species turnover (beta diversity) of the heathlands needs to be taken into account. Several of the sites surveyed for this study are not in conservation reserves, in particular the highly diverse heathlands of the Tutunup area. To preserve what is left of the diversity of this ecosystem, all of the sites included in this study need to be in conservation reserves where they can be more easily managed. More detailed work needs to be completed on the northern part of the coastal plain and along the south coast to provide a complete picture of the wet heathlands of Western Australia.

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Appendix 1. Two-way table produced by TWINSPAN classification of 47 southern Swan Coastal Plain wet heathland quadrats. Underlined species names are the characteristic species of the alliances and associations. Values shown within the table are the Braun-Blanquet cover values for the species. Only species occurring in more than two quadrats are included.

Quadrats	27	29	33	34	35	46	47	28	45	39	40	41	8	7	10	12	13	14	11	15	18	17	19	20	16	21	22	1	2	3	4	5	6	9	23	36	37	38	24	30	31	32	25	26	42	43	44
Alliance	*Pericalymma-Hypocalymma*												*Pericalymma-Regelia*																										*Melaleuca-Cassytha*								
Association (see Table 1)	A1					A2							B1																	B2					B3				C1						C2		
Conostylis serrulata																							1	1		1	1																				1
Phylidrella pygmaea																		1	1																											1	
**Parentucellia viscosa*													1																		1		1													1	
Acacia stenoptera														1	1	1	1														1		1														
Chamelaucium roycei													1	1				1												1	2	2	2	1													
Grevillea diversifolia													2	1					1										1	2	2	2	3														
Leptocarpus aristatus																							1							3	2	2	2														
Loxocarya aff. flexuosa																				1											2	3		2													
**Briza maxima*															1																1	1		1													
Hakea ceratophylla																			1		2	1	2			2	2								1												
Hakea sulcata														1			1		1	1	2	1	1				1	1																			
Isopogon formosus													2	1	2		2		1				1	2			1			1					1												
Regelia ciliata													4		3		3	1	2	2	3	2	3	3	4	1		2	1	2	1		3	3													
Leptocarpus canus													1	2	2	2	2	1	2	2	2							1		2	1																
Leptocarpus elegans															2	1	2		1			1	1					1	1					2													
Melaleuca uncinata														1				1		1	1													1													
Conostylis aculeata																	1		1	1	1	1						1	2																		
Xanthorrhoea gracilis	1	1																	1							1	1	1	1	1		1															
Allocasuarina humilus															1	1	1											1							1												
Calothamnus lateralis							1							2						1	1	2	1				1									1	1										
Dryandra nivea														1	1	1	2		1	1							1						1		1	1	1	1									
Grevillea brachystylis																			1				1	1			1								1												
Helichrysum cotula													1						1												1						1										
Loxocarya fascicularis													1			2	1											1			1						1										
Stirlingia latifolia															1	2	1		2				1			2	2						1		2												
Hibbertia rhadinopoda													1														2								1												
Mesomelaena tetragona														1	1	1		2					1			1	2	1		1					2	1	4										
Synaphea reticulata														1		1	1		1																2	1	1										
Tricoryne eliator													1				1																			1	1										
Daviesia preissii												1																							1	1	2	1									
Boronia dichotoma						1	1		1											1	1			1						1					1	1											
Acacia pulchella		1			1	1	1						1															1	1	1						1	1										
Pericalymma ellipticum		1			1	4	4	3	3	4	4	3	1	4	2	4	4	3	4	4	4	4	3		2	4	4	4	4	4	4	4	4	3	4	3	2	1									
Xanthorrhoea preissii			1	1	2	1	1		1				1	1	2	2		2						1		1	1						1		1	1	1	1									
Adenanthos meisneri	2		1	1	1	1	1		2		1	1	1	1	2	2	1	1					2				1	1	1	1																	
Dampiera linearis	1		1	1			1	1	1				1			1	1					1	1	1	1				1		1				1		1										
Acacia flagelliformis										1	1	1																1	1																		
Evandra pauciflora	1					1	1		3	3	1	2																																			
Acacia semitrullata			1	1	1	1	1			1																																					
Adenanthos obovatus	1	1	1	1	1	2	1	1	1																1	2		1							1												
Dasypogon bromeliifolius	1	2	1	2	3	2	2	2	2																																						
Euchilopsis linearis	1	1	1	1		2	1	1	1	1															1																						
Hypocalymma angustifolium	3	2		2	2	2	2	1	2	1	2	2													2	2									1												
Kunzea ericifolia	1				1	1	1		2	1																																					
Lysinema ciliatum				1							1	2			1																																
Hibbertia vaginata	1		1	1	1							1																																			
**Hypochaeris glabra*		1	1	1																								1																			
Lyginia barbata		1	1	1	2														1																	1		1									
Lepidosperma angustatum					1																	1				1							1								1						
Hypolaena exsulca				1		1	1	1	1	1	1	2			1	1		1	1							1		1							1					2		2					
**Ursinia anthemoides*	1	1	1	1	1																																		1						1		
Melaleuca preissiana						1	1			1																																	1				
Drosera macrantha														1																1						1		1	1					1			
Hakea varia																					2	3		1					1						1		3	2				1			1	1	2
Sphaerolobium medium																				1	1	1	1	1			1		1							1	1	1	1	1	1	1					1
Acacia saligna																														1			1													1	1
Kunzea recurva																																1	1			3	1	4					1	1	2	2	1
Thysanotus patersonii						1	1		1																														1				1	1			
Lepyrodia glauca																													1			1								1	1	1	1	1			
Hakea marginata																																							2				1	2			
Lepyrodia muirii																																								1	1	1	1	1			
Melaleuca viminea																																							4	4	3	2					
Isolepis nodosus																																							2	4	3	2	3	3			
Cassytha glabella											1				1					1			1	1				1	1										1	1	2	2	2	1		2	1
Melaleuca incana																																											2	2	2	2	3
Gahnia trifida																																											1		2	1	1
Sporobolus virginicus																																													1	2	1
Melaleuca hamulosa														1													1	1	2																3	2	2

*Exotic species